

THE MORPHOLOGY AND THE RELATIONSHIPS OF THE LEPTONETIDAE (ARACHNIDA: ARANEAE)

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ABSTRACT

The tracheal apparatus of the Leptonetidae is examined; there are considerable differences between some genera. The taxonomic position of the family is discussed; they can not be related to any family of the "Haplogynae" by known shared derived characters.

INTRODUCTION

Until twenty years ago the Leptonetidae were a small group, known in life only to a few arachnologists. The recent discovery of more than a hundred new forms in the Mediterranean region, East Asia (Japan and Korea) and North America (USA and Mexico) has done little to change this.

Since most of the species are known only from caves, only the few cave specialists have had a good opportunity of examining material.

Much is still to be learned, especially of the biology and reproductive behavior of members of this family; also, the taxonomic position of the Leptonetidae is still unclear.

OBSERVATIONS ON THE RESPIRATORY APPARATUS

Some authors (e.g., Levi 1967:577) have thought the Leptonetidae lungless, although all species examined have indeed normal booklungs (personal observations; Fage 1913:490, Machado 1945:132).

A detailed study of the lungs has not been made. The number of leaves is low (Fage also saw only "quelques feuillets") and in general appearance these lungs are similar to those of some *Ochyrocera*, while in some Erigonidae, Linyphiidae and Theridiidae of similar size (*Diplocephalus*, *Centromerus*, *Porrhomma* and *Theonoe*) the lungs appear more developed. The tracheal apparatus however, which is quite conventional in position, is more interesting than the lungs.

Lamy (1902) found in *Leptoneta microphthalma* Simon a very normal tracheal apparatus with a single slit-like spiracle which communicated with a wide vestibule; from

the vestibule originated four simple tracheal tubes. Machado (1945) found a similar condition in a Portuguese *Leptoneta*; and I in a Mexican *Neoleptoneta* (Fig. 4). Such an apparatus exists in many spiders. A curious Portuguese *Paraleptoneta* (named by Machado in 1951) had instead two clearly separated tracheal spiracles, not united by a vestibule (Machado 1945). Such an apparatus, with simple posterior trachea, is typical of the family Telemidae.

No Leptonetidae I examined had an apparatus of this kind, but three Mediterranean species [*Leptonetela strinatii* (Brignoli), *Sulcia cretica* Fage and *Barusia aesculapii* (Brignoli)—I follow the taxonomical changes proposed by Kratochvil 1978] had an intermediate, undescribed system. In these species there is a wide, normal vestibule, and at each corner there is a spiracle (Figs. 3, 5, 6). The openings of these spiracles are reinforced, and clearly visible with a phase-contrast microscope. It is impossible to say if a slit unites them, as in *Leptoneta* and *Neoleptoneta*; in these forms the slit is a mere fold of the integument and a real opening is not visible. In my opinion it is not especially relevant to ascertain the presence of a functional slit; the most important point is the presence of two reinforced openings which correspond to the two separate spiracles observed by Machado in *Paraleptoneta synthetica*. Machado considered this species primitive; the forms with a vestibule, advanced. The species I observed would then occupy an intermediate position.

The tracheal tubes of *Leptonetela* are characteristic; those of *Barusia aesculapii* and *Sulcia cretica* are somewhat different because of the presence of two large trunks; at the corner of the vestibule from each trunk depart a large number of tracheal tubes.

In the Leptonetidae the respiratory apparatus is thus usually, relatively normal. This is rather puzzling if we compare them with the Telemidae and Ochyroceratidae which also contain small, nonsclerotized and hygrophilous spiders. As in these two families, one might expect the absence of lungs in at least some leptonetids.

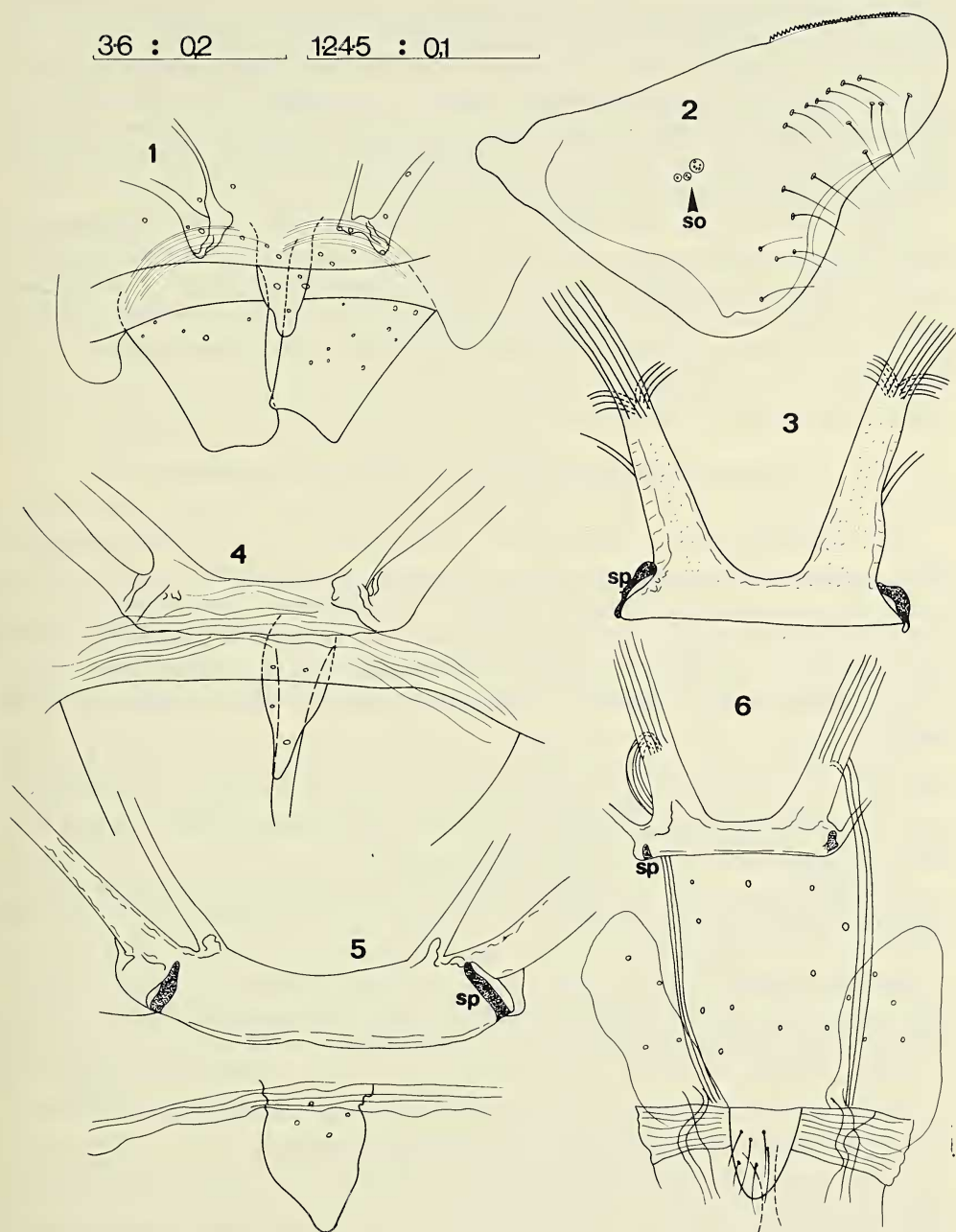
On the other hand the Leptonetidae are more similar, in general size and relative development of the legs, to the larger Ochyroceratidae (*Ochyrocera* and *Althepus*) that have lungs, than to the smaller genera of this family (*Speocera*, *Theotima*, etc.) and to the Telemidae. Unfortunately, as Levi (1967:582) already noted, we know little of the physiology of respiration in spiders, and it is difficult to evaluate the relative efficiency of the lungs and of the trachea. The correlation between hazard of water loss and reduction of booklungs suggested by Levi (1967) is an interesting hypothesis but we need more information on this subject before we will be able to understand why groups which ecologically appear similar do not have the same kind of respiratory apparatus.

I am unable here to discuss the second hypothesis of Levi (1967), that "the trachea of the larger Dysderoidea may represent a phylogenetic character inherited from smaller ancestors."

SOME OTHER MORPHOLOGICAL OBSERVATIONS

Male Genitalia.—The palpal bulb can be expanded, it is not immobile, as that of many Haplogynae. For illustrations of *Leptonetela* see Brignoli (1976). I have also recently observed the same fact in *Paraleptoneta spinimana*.

Female Genitalia.—The vulva consists always of two tube-like spermathecae, whose surface is covered by a glandular tissue and there are no fertilization ducts (the haplogyne condition according to Wiehle 1967); the atrium is relatively complicated and can pro-



Figs. 1-6.—Morphology of the Leptonetidae: 1, *Neoleptoneta caliginosa* Brignoli, tracheal region (apparently there is no vestibule, but this is probably an artifact due to poor preservation of the abdomen); 2, *Leptonetela strinatii* (Brignoli), gnathocoxa showing "sensory organ" (=so); 3, *Sulcia cretica* Fage, tracheal region showing the wide vestibule and the two large lateral trunks; 4, *Neoleptoneta capilla* (Gertsch), tracheal region (note the similarity with *Leptonetela* and the absence of the sclerotized spiracle); 5, *Leptonetela strinatii*, tracheal region [identical is the same region of *Leptonetela kanellisi* (Deeleman-Reinhold)], spiracle = sp.; 6, *Barusia aesculapii* (Brignoli), tracheal region (note the considerable distance from the spinnerets). Scales in mm.

trude through the epigastric furrow. An expanded bulba (Brignoli 1975, Kratochvil 1978) resembles the condition found in some Linyphiidae. On the terminal part of the expanded vulva (which is like an inverted pouch) at each side of a hollow (but not always present) tongue-like structure is (always ?) a small porous plate similar to those found in some Scytodidae and most Pholcidae. The openings of the spermathecae, always difficult to see, are situated on the sides of the expanded (more or less triangular) vulva, near the porous plates (for illustrations see Brignoli 1979).

Gnathocoxae.—On the inner side of the gnathocoxae (Fig. 2) some structures are visible which are similar to the organ believed sensory also observed by Machado (1951) in the Ochyroceratidae. These structures could be identical with the “sexual glands” recently discovered in *Leptoneta microphthalmia* by Lopez and Emerit (1978). Since very few spiders have been examined carefully these structures may be present in most families.

THE TAXONOMIC POSITION OF THE LEPTONETIDAE

Most arachnologists have considered the Leptonetidae to belong to the haplogynes, which may be so if we consider the term “haplogyne” to have no phylogenetic meaning. They may be put in the Araneoidea (Archer 1948, Levi 1967) but no family of the Araneoidea seems related to them. Their expanded palpal bulb (Brignoli 1979) and their tarsal structures suggestive of a paracymbium recall some primitive Araneoidea such as the Tetragnathidae, but they do not seem to share any specialized characters with this family.

Until recently many authors have considered the Leptonetidae related to the Telemidae and Ochyroceratidae, perhaps because both these families are little known to most arachnologists and include small, rare and often cavernicolous species. Each of these three families is characterized by many autapomorphies:

Leptonetidae—six eyes in peculiar position (only exception *Archoleptoneta*); male palpal bulb little sclerotized, ending with many lamellae, expandable; expandable vulva with two spermathecae.

Telemidae—female genitalia with a single, large spermatheca (structurally different from those found in other haplogynes); with spermatophores [their existence, which I recently (Brignoli 1978b:113) suggested, has been demonstrated (Lopez, pers. comm.)]

Ochyroceratidae—chelicerae with median lamella (often with stridulatory grooves); vulva with two spermathecae, often curiously modified (for an explanation of this structure see Machado 1964); median spinnerets with a single spigot.

If we search for other characters we are hampered by our limited knowledge of haplogynes. The structure of the eyes, which has given many phylogenetic clues, has not been investigated in detail in the three families in question. According to Homann (1971) only the secondary eyes (*Nebenaugen*) are present in the families Dysderidae, Sicariidae and Oonopidae (and apparently also in other haplogynes). In the Leptonetidae and in the genus *Speocera* (Ochyroceratidae) the secondary eyes have no canoe-tapetum and are of a primitive type, as are those of the Orthognatha, Pholcidae, Urocteidae and Filistatidae. It can be concluded that the eyes of these families are not specialized.

The valuable paper by Kaestner (1953) on the structure and function of the chelicerae said little on most haplogynes; only some groups with a median lamella are discussed in detail (Filistatidae, Caponiidae, Scytodidae and Pholcidae). Kaestner noted many speciali-

zations (perhaps synapomorphies) in these groups, but the only explanation he could find (a secondary reduction due to the development of peculiar methods of capturing prey) is in my opinion only satisfactory for the Scytodidae.

From the scattered information we have on the development of the haplogynes we come to conclusions similar to those obtained from the eyes: the haplogynes and the Orthognatha (all ?) differ in their embryonic development from other spiders (Holm 1940). However, to share a primitive type of embryonic development is definitely not a synapomorphy.

There are no trichobothria on the tarsi of the Leptonetidae, Telemidae and Ochyroceratidae, but I am unable to estimate the phylogenetic value of this character, which has not been examined in many groups.

The palpi of the males of many Leptonetidae and Ochyroceratidae bear on their articles (femur, patella, tibia or tarsus) large, often transformed, spines or apophyses. Until their function is known it is questionable to consider them synapomorphic as many spiders of different families have similar structures.

Also until we know other haplogynes better, the large rhomboidal colulus and the four independent tracheal spiracles of the Telemidae have to be considered doubtful autapomorphies.

If we search for synapomorphies, we can find only that: (a) the chelicerae of the Leptonetidae and Telemidae are similar, but not specialized [those of the Ochyroceratidae are similar to those of the Scytodoidea (Brignoli 1975)]; (b) the position of the eyes of the Telemidae and Ochyroceratidae is the same as that of many six-eyed spiders; (c) the bulbs of the pedipalps of Telemidae and Ochyroceratidae are relatively simple, as are those of many haplogynes; and (d) the colulus of the Leptonetidae is similar to that of the Ochyroceratidae (and of most spiders). From these facts we can not conclude that these three families are closely related.

I referred the Ochyroceratidae to the superfamily Scytodoidea (Brignoli 1975), slightly different from the group proposed by Bristowe (1938). Recently (Brignoli 1978c) I am including the Filistatidae in the Scytodoidea. While the Dysderoidea seem to share important synapomorphies in the structure of the female genitalia (Brignoli 1975), the Scytodoidea are a much less natural group and may have to be divided.

The position of the Telemidae is still not clear, and much research will be necessary to ascertain if spermatophores are present in other families (I recall here the "strands" seen protruding from the palpal bulbs of some Oonopidae and Tetrablemmidae by Machado 1941, Brignoli 1974).

In 1975 I divided the haplogynes into four groups: one of these should be the Leptonetidae, for which a separate superfamily could be proposed. I still can not find any synapomorphies shared by the Leptonetidae and any other haplogyne family. The Dysderoidea have peculiar female genitalia (Brignoli 1975). The absence of the median lamella of the chelicera in the Leptonetidae (at present the only synapomorphy on which I base the Scytodoidea) excludes them from the Scytodoidea. A superficial examination of the genitalia might suggest relationships between the Leptonetidae and some Scytodoidea with two spermathecae (*Scytodes*, etc.), but in no family of the Scytodoidea has an expandable vulva been found. The specializations of the male tarsus of many Leptonetidae resemble those of some Ochyroceratidae and all Pholcidae, but this apparent synapomorphy is contradicted by the completely different structure of the female genitalia in these three families (personal observations on about 100 species in 25 genera of both Pholcidae and Ochyroceratidae).

The other families which I include provisionally in the Scytodoidea (Sicariidae, Diguettidae, Plecteuridae, Tetrablemmidae, Pacullidae and Caponiidae) do not share any derived character with the Leptonetidae.

Perhaps we will still find the relatives of the Leptonetidae. The curious genus *Physoglenes* Simon, 1904 (of which unfortunately no specimens survive) was thought to be a leptonetid by Simon, a theridiid by Fage, and a pholcid by Petrunkevitch (Brignoli 1978a). Future finds of this genus could be quite revealing.

To summarize, the Leptonetidae are not close to any other haplogynes and may belong in their own superfamily.

ACKNOWLEDGMENTS

I thank Norman I. Platnick and William A. Shear for their suggestions, and especially Herbert W. Levi for his help in editing this paper. I have had an interesting exchange of ideas on the Telemidae with Dr. A. Lopez.

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